SEX-LINKED INHERITANCE IN ULVA

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In an earlier report (Föyn, 1959) mention was made of two autosomal mutants, Slender (*S1*) and long (*1*), both of which spontaneously arose in cultures of *Ulva mutabilis* and both of which exhibit sex-controlled manifestation. Found among the young gametophytes from a crossing between the two mutants was a small dwarfed individual entirely different from the types hitherto known. The individual was isolated and proved to belong to the − -sex. In order to determine whether it was a matter of a new hereditary type or only a phenotypical abnormality, the gametes were put to parthenogenesis. The new germ plants were all of the same kind as the mother plant, and thus probably represented a new mutant. As described earlier (Föyn, 1958) parthenogenesis in this species is normally connected with doubling of the chromosome number. The parthenogenetic plants therefore became diploid and produced (haploid) zoöspores. Figure 1 shows a few stages in their development towards gametophytes.

FIGURE 1. *Ulva mutabilis.* Young *dw S1* individuals from zoöspores. a, 10 days old; b, 17 days old.

The gametophytes were fertile after a good month and they were then crossed with the wild-type. The zygotes germinated immediately to germ plants of the sporophyte generation. As Figure 2 shows, they resemble the sporophyte germ plants after crossing between the Slender-type and the wild-type but diverge from them by the tapered top and the weakly developed rhizoids which do not grow out from the entire basal part, but only from a single point medially below this. With some germ plants the basal part can also grow one or a few short branches such as in the individual on the right of the figure, but this is rare.

The hybrid sporophytes when about 2½ months old formed zöospores. The plants had then grown to a length of 25–30 cm., flat, and with even width (ca. 1 cm.) band. Zoöspores from one of the plants were transferred to a petri dish

which was thereupon placed in darkness until the following day. The zoöspores had by then become distributed evenly over the bottom of the dish and had affixed themselves to the glass. Inspection 10 days later found the bottom over-grown by various types of germ plants. A precise count was taken within a circle-shaped area of 2.3 cm. diameter, and the various types were at the same time separated, each plant being loosened from the under-bedding with the aid of a glass needle and transferred to a new petri dish. Altogether, within the limited area 728 germ plants were found. Of these, 189 belonged to the wild-

FIGURE 2. *Ulva mutabilis.* Twelve-day-old sporophytes from a cross between a *dw S1* gametophyte and a gametophyte of the wild-type.

type and 138 to the Slender-type. The remaining 401 consisted for the greater part of germ plants of the same appearance as in Figure 1a and thus resembled the pristine mutant plant completely. A smaller number were more simple, built more clumpily, and were only weakly ramified (Fig. 3a). Every transition between the two types was found, however, and an assortment into two distinct groups had, therefore, to be abandoned. All of them were reckoned as belonging to the mutant type. Thirty-six germ plants could not be identified; they were, partly, of different shape and dissimilar to the types hitherto known. The plants

were accordingly carried forward to sex-maturity and the gametes were put to parthenogenetic development. A survey of the parthenogamete plants 14 days later showed that not one of them represented new mutants. Four belonged to the wild-type, 21 to the Slender-type and 11 to the mutant-type. The final result of the count was therefore:

wild-type:	193 individuals (26.51%)
mutant-type:	376 individuals (51.65%)
Slender-type:	159 individuals (21.84%)

It is therefore a matter of a crossing with two independently segregating factors of which the one is *S1*. The other has been designated *dw*. Half of the 376 germ plants of the mutant type must have both the chromosomes with *S1* and the chromosome with *dw* the other half, only the chromosome with *dw*.

Three dishes with altogether 220 mutant germ plants were placed under the source of light and, gradually, as the plants grew, the largest were isolated, carried forward to sex-maturity, and crossed with the wild-type. It soon became

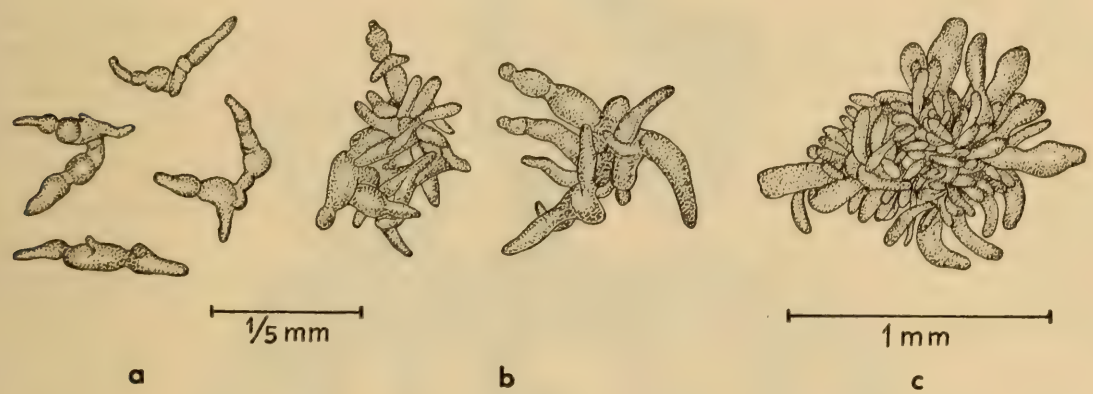

FIGURE 3. *Ulva mutabilis*. Young *dw* individuals from zoöspores. a, 12 days old; b, 19 days old; c, 30 days old.

evident that *dw S1* individuals grow much more rapidly and, therefore, become fertile earlier than *dw*-individuals. The first crossings all resulted in sporophytes of the same kind as the mother sporophyte (Fig. 2). It was only after 84 plants had been tested that the crossings between the three successive individuals and the wild-type gave another result, namely, sporophytes of the wild-type. Upon the formation of zoöspores eleven weeks later, they segregated into the mutant and the wild-type in the ratio 1 : 1. A precise count was not taken as already at the first glance into the microscope it was evident that the two types were represented equally strongly.

For each crossing undertaken, the gametes of the mutant partner were put to parthenogenesis. In the first 84 cases mentioned the gametes developed, as expected, mainly to germ plants of the ramified type, but also a few developed to individuals of the simple type. After the three crossings following, however, the ratio was reversed: most of the parthenogamete plants became simple whereas only a few became considerably ramified. Even if weak or no ramification accordingly must be said to be a typical character of the pure *dw* germ plant,

it is no certain distinguishing feature. One of the three above-mentioned dishes having mutant germ plants contained only individuals of the simple type, altogether 20; 13 of them later yielded gametes, 10 proved to be pure *dw* plants and the remaining three, *dw S1* individuals. The two other dishes each contained 100 germ plants, chosen casually, without regard to type or size. Of these, altogether 197 have been tested in crossing with the wild-type with the following result: 118 were *dw S1* individuals, 79, *dw* individuals.

It is apparent from Figures 3c and 4 that the *dw* plants also later become considerably ramified, frequently much more so than *dw S1* plants. The fertile *dw* individual looks like a rosette of young wild-type plants grown together. The thallus is dark green, often folded, and gives a stunted impression. The two layers of cells are either grown together throughout or are separated from each other along the border of the thallus. The thickness of the layers is greater than

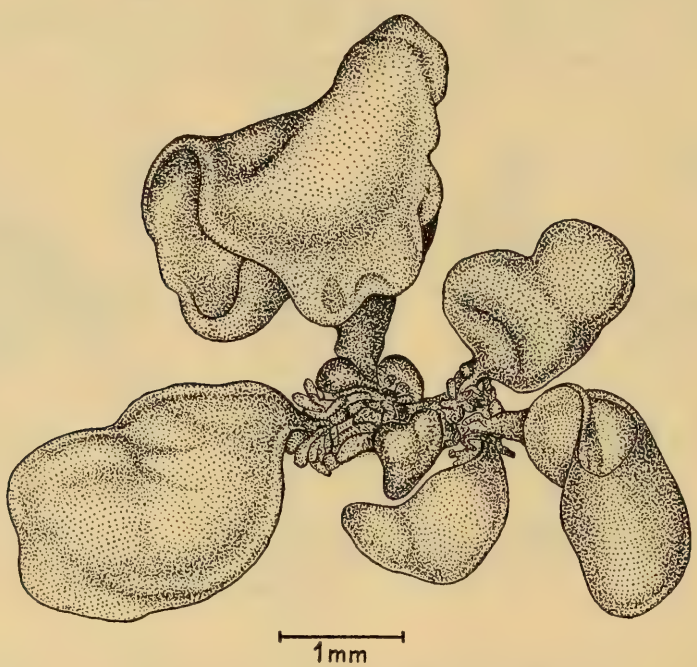

FIGURE 4. *Ulva mutabilis.* A full grown and fertile *dw* sporophyte. Three months old.

in the wild-type. The rhizoids are weakly developed or are not at all distinguishable. It is because of this dwarf-like appearance that the mutant factor has been termed *dw*.

The fertile *dw S1* plants much resemble the *dw* plants. Nor do they become larger than these but the two layers of cells are often free throughout and, partially, distend strongly from each other. Most frequently, they have the usual green colour.

More interesting than these results, however, was that all the 210 mutant individuals (both *dw* and *dw S1* individuals) which had been carried forward to sex maturity proved to belong to the — -sex. Investigation was therefore made as to how the 193 individuals of the wild-type and the 159 Slender individuals behaved in this respect. Where the latter are concerned, it had already been

observed during the counting that most of them were ramified which, with this mutant, is a quite certain sign that they are + -individuals (see below). Only 61 were unramified and these were therefore isolated and carried forward to sex maturity. All of them revealed themselves as + -plants. Of the wild-type, 100 individuals were tested with regard to sex, all with the same result, namely, that they belonged to the + -sex. Also in different later crossings which, in another connection, have been performed with *dw*-plants, individuals with the *dw* factor have proved to be of the − -sex. The factor *dw* must therefore be located in the same chromosome as the factor(s) for the − -sex.

It has not been possible to establish cases of crossing-over between *dw* and the sex-factor(s). The crossing best suitable for the discovery of such cases is that between *dw S1* and *dw*$^+$ *S1* individuals. The crossing can naturally only result in the same types of gametophytes as the parents, and, apart from eventual cross-overs, the *dw S1* plants will belong to the − -sex and the *dw*$^+$ *S1* plants, the + -sex. As described earlier (Föyn, 1959) the germ plants of the − -sex of the Slender race are always long, slim and unramified, whereas the germ plants of the opposite sex can either be like the − -individuals or be small and considerably ramified. This variation rests upon hitherto unknown environmental conditions, as + -zoöspores from one and the same sporophyte after one swarming can develop to germ plants, all of which are small and ramified, and, after another, to both ramified and unramified, or to unramified germ plants only. In the cases where the first possibility is realized from the + -zoöspores of *dw dw*$^+$ *S1 S1*-sporophyte, naturally a − -individual of the Slender-type will immediately become evident. Of the 14 petri dishes with their bottom wholly covered by haploid germ plants from two *dw dw*$^+$ *S1 S1*-sporophytes, three contained exclusively small and ramified germ plants. In the one dish the germ plants originated from the one, and, in the other two, from the second sporophyte. In two of the dishes there were more than 4000 individuals, in the third, more than 5000 individuals; thus, from among more than 6500 *dw*$^+$ *S1*-individuals, not a single cross-over was observed.

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Summary

A recessive sex-linked mutant is described that arose spontaneously in cultures of *Ulva mutabilis*. It has not been possible to establish cases of crossing-over between the sex chromosomes.

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